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Last Larval Instar and Mature Oocytes of the Old World Cleptoparasitic Bee *Stelis murina*, Including a Review of *Stelis* Biology (Apoidea: Megachilidae: Megachilinae: Anthidiini)

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ABSTRACT

Herein we describe the mature oocyte and last larval instar of *Stelis* (*Stelis*) *murina* Pérez, a cleptoparasite associated with *Osmia* (*Pyrosmia*) *submicans* Morawitz near Ismailia, Egypt. The mature oocyte is compared with that of *Stelis* (*Stelis*) *elongativentris* Parker and found to be approximately equal in size. The mature oocyte of *S. murina* is also very close in size to that of its host, an unusual phenomenon in host-cleptoparasite relationships in bees.

A review and analysis based on literature accounts of what is known about the mode of cleptoparasitism of *Stelis* is offered. Added are observations on the biology of *Stelis murina* resulting from our fieldwork.

The mature larva of *Stelis murina* is described and found similar but not identical to those of other known *Stelis* larvae. We also include a preliminary key to the genera of cleptoparasitic megachilids based on known mature larvae and also a summary describing the modes of cleptoparasitism by these taxa.

INTRODUCTION

This paper describes the mature oocyte and the diapausing, last larval instar of the cleptoparasitic bee *Stelis* (*Stelis*) *murina* Pérez and presents statistics regarding the female's ovaries and mature oocytes. We also compare its mature oocyte with the egg/mature oocyte of its host *Osmia* (*Pyrosmia*) *submicans* Morawitz. This contribution is another treating cleptoparasites associated with solitary bees that the second author is

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attempting to rear because of their importance in pollinating Egyptian clover (*Trifolium alexandrinum* L.) and alfalfa (*Medicago sativa* L.) in the vicinity of Ismailia, Egypt.

Our wish is to explore the basic biology of these cleptoparasites to understand their biological relationships with their hosts and their phylogenetic relationships with the numerous other cleptoparasitic bees found on all continents supporting bee populations. Basic information gathered from these studies is important because these animals impinge upon the populations of pollinators of Egyptian crops and therefore on the well-being of the Egyptian people and their economy.

In addition to *Osmia submicans*, the solitary bees being reared by the second author are cavity nesters belonging to the Megachilidae, including *Megachile* (*Pseudomegachile*) *nigripes* Friese, *M.* (*Pseudomegachile*) *cinnamomea* Alfken, *M.* (*Pseudomegachile*) *flavipes* Spinola, and *M.* (*Eutricharaea*) *minutissima* Radoszkowski. They are often found in astounding numbers flying with their cleptoparasites about nesting areas on vertical surfaces constructed from dried mud, such as buildings and walls (Rozen and Kamel, 2007: fig. 1). The cleptoparasites, their known hosts (in parentheses), and references to our studies of them are as follows: *Radoszkowskiana rufiventris* (Spinola) (*M. nigripes*) (Rozen and Kamel, 2007); *Coelioxys* (*Liotherapis*) *decipiens* Spinola (*M. nigripes*, *M. flavipes*) (Rozen and Kamel, 2007); *C.* (*Allocoelioxys*) *coturnix* Pérez (*M. minutissima*) (Rozen and Kamel, 2008); and *Sapyga luteomaculata* Pic (*O. submicans*, *M. minutissima*) (Rozen and Kamel, 2009). All the cleptoparasites are members of the Megachilidae, except *S. luteomaculata*, which belongs to the vespoid family Sapygidae. *Stelis murina* parasitizes nests of *Osmia* species in Egypt and elsewhere (e.g., Westrich, 1989).

The ecological interrelationships of this assemblage of hosts and cleptoparasites beyond their cleptoparasitic associations have yet to be studied in detail. When this is done, it will likely confirm our suspicions that the initial colonization of vertical nesting areas in this local geographic region is performed by *Megachile nigripes* and that all other nesting species arrive to use abandoned nests of this species. Cleptoparasites, of course, follow their hosts. Because well-established nest sites show considerable surface deterioration due to the mining activities of *M. nigripes* (e.g., fig. 2; Rozen and Kamel, 2007: fig. 2), one might assume that only old structures are occupied. This is certainly not always the case since fairly recent surfaces are colonized. As one would expect, the relative abundance of nesting species (and cleptoparasites) varies from one site to another, no doubt due in part to the timing of chance arrivals of the secondary nesters.

The geographic limits of this association of cavity nesters and their cleptoparasites is unknown though it obviously relies on the availability of nesting sites adjacent to agricultural fields supporting clover and/or alfalfa. Certainly the geographic ranges of the component species are extensive, going far beyond this local region (http://www.discoverlife.org). For the present, this particular assemblage of species seems to be held together by the availability of food, a convenient cavity maker in the form of *M. nigripes*, and the substrate it uses.

DESCRIPTION OF SITE AND METHODS

Dense nesting sites of these bees are scattered widely in the area west of Ismailia, especially in the numerous small villages around the towns of Tel el-Kebir (N 30°33′01″ E 31°46′48″) and El-Huseiniya (N 30°51′21″ E 31°55′11″) (fig. 1). We examined four specific sites for this study. Sites 1 and 2 associated with Tel el-Kebir were at N 30°32′04″ E 31°53′08″ and N 30°32′15″ E 31°55′51″, respectively; sites 3 and 4 associated with El-Huseiniya were at N 30°52′05″ E 32°00′11″ and N 30°51′52″ E 32°03′46″, respectively. This part of the study was carried out from May 12–20, 2008. However, the mature larvae described toward the end of this paper were retrieved on an earlier field trip in September 2006.

Nests at these sites, though numerous, are usually difficult to study because of one or a combination of the following: (1) they may be in a structure still being used by humans; (2) they may be in areas of dense human

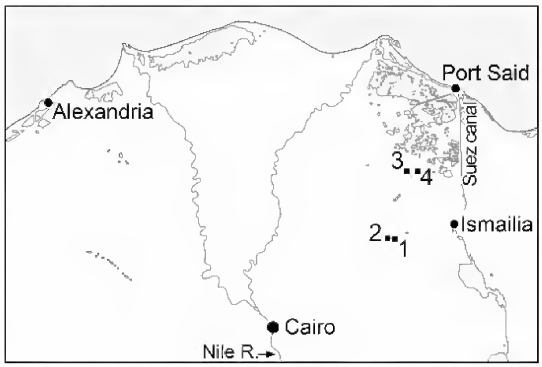


Fig. 1. Map showing the position of study sites 1 and 2 (Tel el-Kebir) and sites 3 and 4 (El-Huseiniya) in the vicinity of the Nile River Delta, northern Egypt.

populations not amenable to careful excavation; (3) the nesting substrate may be too difficult to excavate because of the density and strength of dried mud; and (4) discovery of active nests in a substrate riddled with empty burrows can be challenging.

These problems have now been circumvented thanks to S.M.K.'s development of large nesting panels, i.e., oversized trap-nests, which are deployed in areas where a high density of females are searching for nesting cavities. The panels consist of row after row of preformed cavities filled with paper straws of appropriate diameter to accommodate nesting bees.Once a sufficient numbers of nests are in place, the panels can be transported to Suez Canal University for study, or the nesting straws can be removed individually in the field and taken to the laboratory for examination. These panels and nesting straws have been described and illustrated by Rozen and Kamel (2008, 2009), and on the web (http://www.pollinatorparadise.com/Egypt.htm).

Nests that bees construct in nesting straws are easily opened compared with nests hidden in dried mud. One merely pulls a straw from the polystyrene-foam panel board with pliers or Cresson pinning forceps and takes it (with as many more straws as seem necessary) to the laboratory. After being sliced lengthwise with a utility knife, the two halves are split apart to reveal the nest contents, which can be examined under a stereomicroscope in the controlled environment of the laboratory.

Immatures were examined with a Hitachi S-5700 scanning electron microscope (SEM) after they were critical-point dried and coated with gold/palladium.

REVIEW OF THE MODE OF CLEPTOPARASITISM IN *STELIS*

In our study of the biology and mature larva of *Stelis murina*, we reviewed previously published accounts of these maters regarding the following species in the genus: *S.* (*Stelis*) *chlorocyanea* (Cockerell) (Rust and Thorp, 1973); *S.* (*Stelis*) *elongativentris* Parker (Rozen, 1987); *S.* (*Stelis*) *lateralis* Cresson (Graenacher, 1905, as *S. sexmaculata* Ashmead); Michener, 1955); *S.* (*Stelis*) *minuta* Lepeletier and Serville (Verhoeff, 1892: fig.; Enslin, 1925: fig. 10); *S.* (*Stelis*) *montana* Cresson (Torchio, 1989); *S.* (*Stelidomorpha*) *nasuta* (Latreille) (Friese, 1923; Maneval, 1937); *S.* (*Stelis*) *ornatula* (Klug) (Enslin, 1925; Micheli, 1935: fig. 10); *S.* (*Stelis*) *punctulatissima* (Kirby) (Westrich 1989: 173); *S.* (*Dolichostelis*) *rudbeckiarum* Cockerell (Parker et al., 1987); *S.* (*Stelis*) *vernalis* Mitchell (Mathews, 1965). Paramount in completeness among these was Rust and Thorp's (1973) investigation of *S. chlorocyanea*, and Torchio's (1989) detailed study of *S. montana*. Despite these reports, the modes of parasitism of the genus are not fully understood, although two different modes seem to exist, and possibly a third mode may also be present. The reason for this review was to identify what is known and not known about cleptoparasitism in the genus so that future studies can be directed toward completing our understanding of this matter.

This review does not make comparisons with *Hoplostelis*, one species of which had its biology (Bennett, 1966) and immature stages (Rozen, 1966) described. That genus is no longer considered closely related to *Stelis*, as also is the case for *Austrostelis*, whose immatures are unknown (Michener, 2007).

Modes of Parasitism: The most common mode of parasitism in the genus known so far involves species belonging to the subgenus *Stelis*. Eggs of these species are introduced into cells that are still open (i.e., not yet closed by the female host), and their larvae at one or more stages kill the host immatures and the

immatures of any competing cleptoparasites. As a result, only a single *Stelis* (*Stelis*) larva reaches maturity despite the number of *Stelis* eggs deposited in the cell. With most species, we have been unable to determine whether multiple parasitism results from a single parasite laying more than one egg at a time on a single visit or whether more than one parasitic female has visited the nest. Torchio (1989) convincingly was able to observe the single-egg depositions of *S. montana* within glass-tube nests inserted in observation boxes even though a female was "physically capable of depositing more than one egg per host cell per visit." Friese (1923) considered multiple-egg depositions by a cleptoparasitic bee in a single cell to be unique for *S. nasuta* among all cleptoparasitic bees. However, this matter needs to be explored more fully because multiple cleptoparasitic eggs in single cells is a common phenomenon in this genus, as suggested by the following: Rust and Thorp (1973) pointed out that 50% of cells parasitized by *S. chlorocyanea* early in the season held two *Stelis* eggs. Graenicher (1905) described three larvae of *S. lateralis* feeding in a cell and then killing one another until only one was left. Michener (1955) studied a nest in which two eggs of *S. lateralis* were placed in the top host cell and single eggs were deposited in each of the remaining nine cells. Rozen (1987) observed two cells each with two eggs of *S. elongativentris*.

All these cases could have been a result of depositions by either a single *Stelis* female or separate females. Adding to this uncertainty, biological information on this matter is lacking for the five other subgenera of *Stelis* currently recognized (Michener, 2007). (Interestingly, multiple-egg deposition by a single female has been reported for cleptoparasitic Sapygidae [Torchio, 1972; Westrich, 1989; Rozen and Kamel, 2009], in which only one larva normally survives beyond the first stadium.)

Stelis (*Stelidomorpha*) *nasuta* is the unique example of the second mode of cleptoparasitism as reported by Friese (1923) and separately by Maneval (1937). Females of this species deposit a number of eggs into the cell of the much larger *Megachile* (*Chalicodoma*) *parietina* (Geoffroy) (referred to as *Chalicodoma muraria* Latreille), whose provisions are adequate to feed up to six larval *S. nasuta*, as evidenced by the discovery of their cocoons in single host cells. Neither author explained how the host offspring was eliminated: by assassination from *Stelis* larvae (as in the first mode described above), by removal by the *Stelis* female, or through starvation resulting from competition with numerous feeding *Stelis* larvae. Assassination by *Stelis* larvae, though occurring elsewhere in the genus, seems unlikely, since larvae of *S. nasuta* are obviously not aggressive toward one another. We question whether a cleptoparasite larva would be able to distinguish between the early instar of siblings and that of the host. It would be interesting to learn whether *S. nasuta* has special modifications of its ovaries (such as increase in ovariole numbers) to produce so many mature eggs at one time (see section on Ovarian Statistics, below).

The possible third mode of cleptoparasitism is that of *Stelis* (*Dolichostelis*) *rudbeckiarum*, as described by Parker et al. (1987). They reported on a female of this species opening an entrance plug of resin by first removing the resin and storing it as a lip around the entrance opening. She then removed a small amount of host provisions and the next day closed the entrance with the stored resin. Michener (2007) proposed that these actions may be similar to the behavior of the related *Euaspis*, females of which open closed nests, remove and destroy host immatures, and rebuild the nests, provisioning them with the hosts' food (Iwata, 1976).

Timing of Egg Deposition: As Torchio (1989) reported in his account of the biology of *Stelis montana*, "this species, like other *Stelis*, enters only open cells to deposit its eggs on partly completed host provisions." Rust and Thorp (1973) clearly stated that only host cells that are still open are attacked, and this act takes place "at nearly any stage of provisioning after the pollen mass is formed, and even after the *Osmia* lays her egg on top of the provisions." Although they did not state that female hosts do not attempt to remove or kill the parasite eggs even when it is deposited on the surface of the provisions next to hers, we assume that they would have mentioned such an observation if seen. Studies of other species of *Stelis* s.s. are less informa-

tive but give no information that suggests that closed cells are attacked.

SEQUESTERING CLEPTOPARASITIC EGG: Most authors state or imply that eggs of *Stelis* are hidden in the provisions or between the provisions and cell wall (Enslin, 1925; Höppner, 1904; Michener, 1955; Rozen, 1987; Verhoeff, 1892). However, while reporting similar information for *Stelis chlorocyanea*, Rust and Thorp (1973) added that "eggs placed on top of the provisions are placed adjacent to or on top of the host's egg...." Furthermore, Graenicher (1905) stated that the egg of *S. lateralis* (as *S. sexmaculata*) were occasionally found next to the host egg on the surface of the larval food. These observations suggest that the parasitic female entered the cell while the host was away, perhaps gathering closure material, and that the host female on return did not inspect the cell. This would not be surprising since a similar explanation has been postulated for the egg deposition habits of a *Radoszkowskiana* and some *Coelioxys*, in which the cleptoparasite first instar, still mostly covered by its chorion, kills the host egg (Rozen and Kamel, 2007, 2008).

NUTRITION REQUIREMENTS OF FIRST INSTARS: An interesting question regarding those cleptoparasitic bees whose first instars consume the host eggs/larvae: Is the nutritional content of the host important for the ongoing development of the first instar? Mathews (1965) gave evidence that a larva of *Stelis vernalis* developed normally even when its host immature had been removed previously by the investigators. Torchio (1989) confirms this situation in the case of *S. montana*. Consumption or partial consumption of the host immature and of other cleptoparasitic larvae would seem only to be insurance against competition for the stored provisions.

ANATOMY AND BEHAVIOR OF HOSPICIDAL (I.E., HOST-KILLING) LARVA: An unresolved problem regarding existing accounts of the biology of the various species of the subgenus *Stelis* is the lack of clarity as to which larval stadium (or stadia) assassinates the host, and in the apparent inconsistencies in mandibular morphology from one species to the next. In the case of *S. lateralis*, the mandibles are acutely pointed "throughout larval life" (Michener, 1955). At a later stage (not identified, but not the first), it encounters the host larva and kills it. With *S. elongativentris*, the mandibles are reported to be bidentate in the first and last larval instars, but as Rozen (1987) pointed out, "Because of short bidentate mandibles and sedentary activity pattern, the first instars seemed incapable of killing the host eggs or larvae...." Because Rozen was unaware at that time that first instars of many bees remain pharate and quiescent within the egg chorion (Baker, 1971; Torchio, 1987; Alves dos Santos et al., 2002), we now have reexamined the putative first-instar specimen and discovered that not only did the body cavity contain pollen grains (hence, it had started eating and was no longer quiescent [Torchio, 1989]), but also there was no line of minute spicules on each side of the body just above the spiracular line (as often found on first instars [Rozen et al., 2006; figs. 14, 15]). Hence it seems likely that, despite its minute size, it was not a first instar. However, it was an early instar, and, therefore, mandibles of all instars of *S. elongativentris* are likely bidentate. With both *S. lateralis* and *S. elongativentris*, we now suspect that the last instar may be hospicidal but presumably not the first instar. Information concerning the behavior of other instars is lacking.

In the case of *Stelis chlorocyanea* (Rust and Thorp, 1973: figs. 7–12) the uncertainty regarding the correct identification of the presumed first instar discussed above remains a problem, but it too is an early instar. In this case both it and the subsequent instar (ibid.: figs. 13, 14) have bidentate mandibles, but the last instar mandible (ibid.: figs. 20–23) is "unidentate and falcate," thus suggesting that this could be a hospicidal instar. The authors allow that earlier instars (including the first) are also capable of killing the host immature with the statement: "The lack of raptorial mandibles in the first instar *Stelis* larva is compensated by the aggressive behavior which persists throughout its larva life."

Torchio (1989) identified all of the larval instars of *Stelis montana* and correlated them with behavioral activities. The first instar remained pharate within the chorion, presumably ingesting only embryonic fluid. With the shedding of the remnants of the chorion and the first instar exuviae, the second instar starts feeding on the stored provisions followed a day later by the transformation to the third instar.

A day later it becomes a fourth instar and continues to feed for another day and a half. During the first four larval instars its mandibles are bidentate and the larval is described as "sessile." The duration of the fifth stadium is 7 to 15 days. The larva is now "mobile", behaves aggressively to external stimuli, and the mandible has a single apical point. This then is the single hospicidal instar that attacks host and other cleptoparasitic larvae.

Resolution of the differences in these accounts will come about when studies of the various species (1) are carried out by identifying all larval stadia of each species and (2) are correlated with the behaviors each instar, as has been demonstrated by Torchio's (1989) investigation.

BIOLOGICAL OBSERVATIONS

When we started this study, we hoped to inquire into the mode of parasitism of *Stelis murina*, but the low rate of cleptoparasitism made it impossible to encounter young larvae of *S. murina*. The relatively high incidence of parasitism by *Sapyga luteomaculata* Pic (Sapygidae) in the cells of *Osmia submicans* indicates that it is a more successful cleptoparasite than *S. murina*, probably because its aggressively rapacious first instar can successfully eliminate both host offspring and those of *S. murina* (Rozen and Kamel, 2009).

However, we made several biological observations worthy of note. As stated before, we assume that *Megachile nigripes* was responsible for the primary excavations at the nesting sites. Females of that species provided the preformed cavities that permitted other species, including *Osmia submicans*, to build their nests after the first generation of *M. nigripes* emerged and evacuated their nests. At one point we parked a white pickup truck near the grain storage building at Site 4 in 2008 (figs. 1, 2). The truck's hood, which was close to the building, was pelted during our stay with small, irregular clumps of coalesced sand, many of which adhered to the hood even after we drove many kilometers. This debris was material excavated from the adobe wall and dropped presumably by females of *M. nigripes*. Its tendency to clump and later to adhere to the vehicle suggests that females use nectar to soften the adobe, and the nectar on drying causes adherence. We also noticed that we were occasionally pelted personally by these sandy particles and that the ground close to the building was shallowly covered with them as well.

Because we never found more than one *Stelis* cocoon in a host cell, we conclude that a female of this species, like the other members of its subgenus, either deposits only a single egg in a cell or its larva kills kindred larvae so that only one matures.

The cocoon of *Stelis murina* was described, illustrated, and compared with that of *Sapyga luteomaculata* Pic (Rozen and Kamer, 2009). The larval feces of these two cleptoparasites, which are voided before the inner walls of the cocoons are spun, are clearly different. Those of *S. luteomaculata* are large, ovoid, dark brown to nearly black, and often exhibit a taillike process (Rozen and Kamel, 2009: fig. 6). The fecal pellets of *S. murina* are small (maximum length 0.6 mm), two to three times as long as their maximum diameter, pale tawny, and "tailless." The elongate, pronounced (i.e., sharply rising from the anterior end of the cocoon) nipple of cocoons of this *Stelis* seems to be characteristic of other species in the genus as well as of a cocoon of *Hoplostelis* (*Hoplostelis*) *bilineolata* (Spinola) (specimen from Trinidad, in the collection of the A.M.N.H.). The *Stelis* species with the pronounced nipple in addition to *S. murina* are as follows: *S. chlorocyanea* (Rust and Thorp, 1973); *S. minuta* (Enslin, 1925: fig. 10); *S. ornatula* (Enslin, 1925; Micheli, 1935: fig. 10); *S. nasuta* (Maneval, 1937); *S. punctulatissima* (Westrich, 1989: 173); *S. rudbeckiarum* (Parker et al., 1987: fig. 6); *S. vernalis* (Mathews, 1965); unknown *Stelis* species in A.M.N.H. collection from Arizona: La Paz Co.: 2–8 mi E. Parker, V-9-1963 (M.A. Cazier and M. Mortenson), from galls on *Hilaria rigida* (Thurb.), hereinafter referred to as "unidentified Parker, AZ, specimens/material"; and apparently *S. lateralis* (Michener, 1955)[3]. These species all presumably have one cocoon per host cell, except Maneval (1937) reported that *S. nasuta* had three cocoons per cell in two cells from the same

[3] Although Torchio (1989) did not describe or illustrate the cocoon of *Stelis montana*, he presented a detailed description of how it is constructed.

Fig. 2. The grain storage building at El-Huseiniya, site 4. Note erosion of adobe wall caused by nesting bees and hood of white pickup truck, lower left; see text for explanation.

nest, and Friese (1923) said the same species had a maximum of six eggs per cell (see above). The large body size of its host, *Megachile* (*Chalicodoma*) *parietina*, compared with that of *S. nasuta* supports the idea that multiple individuals of this cleptoparasite may normally coexist in a single brood chamber by sharing a common food mass.

A noteworthy feature of adult *Stelis murina* was the thick, rigid sclerotization of its integument that we detected when we dissected its metasoma to study its ovaries. Its integument contrasted distinctly with that of *Osmia submicans* (and numerous other bees) in which the sclerites are softer and more elastic. A thick, rigid integument is, of course, characteristic of a number of other adult cleptoparasites (e.g., *Coelioxys*, *Sphecodes*), and, as in *S. murina*, such an integument often bears numerous external pits, presumably to entrap the sting apices of host females so that host stings cannot find soft, penetrable conjunctiva. The pronounced transverse pregradular troughs of *S. murina* almost certainly serve the same purpose.

OVARIAN STATISTICS

Stelis murina is the second species of this genus for which ovarian statistics are known. The first was the New World *S.* (*Stelis*) *elongativentris* (Alexander and Rozen, 1987: table 1, as *Stelis* sp.; Rozen: 2003: table 1), a cleptoparasite of *Ashmeadiella* (*Chilosmia*) *holtii* Cockerell. Table 1 repeats the ovarian statistics of *S. elongativentris* and presents those of *Stelis murina* and its host *Osmia submicans*.

We dissected and examined ovaries of eight females of *Stelis murina*, each of which had three ovarioles per ovary (an invariable

TABLE 1
Egg Indices, Number of Mature Oocytes, and Number of Ovarioles of *Stelis elongativentris*, *S. murina*, and *Osmia submicans*

Taxon	Egg index	Total mature oocytes per specimen	Mature oocytes per ovariole	Ovariole formula	No. of specimens
*Stelis elongativentris**	0.61*	2.67*	0.44*	3:3*	3*
Stelis murina	0.64	2	0.33	3:3	6
Osmia submicans	0.71	1.25	0.21	3:3	4

* From Alexander and Rozen, 1987: table 1.

number for Megachilidae to date). In two of these females, the ovaries were underdeveloped because none of the oocytes was greatly enlarged, and the females' wings showed no wear. Consequently, these juvenile adults were excluded from further consideration. The remaining six females each had a total of two mature oocytes, i.e., 0.33 mature oocyte per ovariole (table 1), somewhat fewer than those of *Stelis elongativentris*, and in general fewer compared with the figures for most cleptoparasitic bees (Rozen, 2003: table 1).

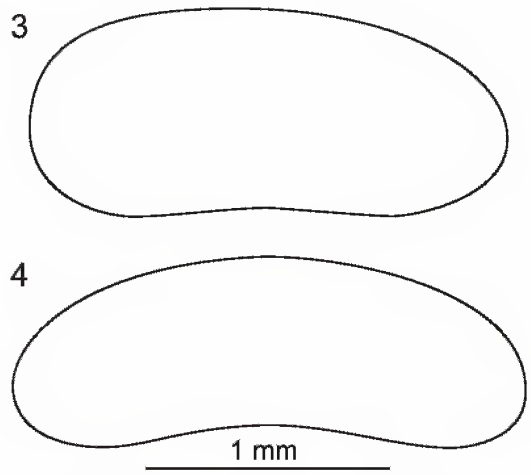
The average egg index of these six specimens was 0.64, only slightly higher than the egg index of *Stelis elongativentris* of 0.61. The egg index, a way of comparing egg sizes of bees irrespective of relative differences in female body size, was developed by Iwata and Sakagami (1966). It is calculated by dividing the length of the largest mature oocyte or egg (= E) of the female, by the distance between the outer rims of the female's tegulae (= M), i.e., E/M = egg index. In the same paper, Iwata and Sakagami (ibid.: table 2) offered a classification of five categories of egg indices (*dwarf*, *small*, *medium*, *large*, and *giant*) based on their ranges of the indices. The egg indices of *S. murina* and *S. elongativentris* are close together in the small category, defined as ($0.50 < E/M \leq 0.75$) (for further explanation, see Rozen, 2003).

We also examined the ovaries of 10 specimens of *Osmia submicans*. Six of these lacked mature oocytes, and, therefore, they, as juvenile adults, were not included in the comparison, although all had an ovarian formula of 3:3, i.e., three ovarioles per ovary. These specimens tended to be less worn, and none carried pollen, whereas those with a mature (or nearly mature) oocyte often showed more wing wear and some carried pollen. We also recognized a difficulty in determining maturity of oocytes since their sizes seemed rather variable. Probably some of those selected were not fully mature, as indicated from a sample of eggs taken from cells, which had an average length of 2.29 mm and an average maximum diameter of 0.77 mm (N = 4), contrasting with the length (2.13 mm) and maximum diameter (0.67 mm) of the mature oocytes given below. Thus, the average dimensions for mature oocytes of *O. submicans* tend to be understated, which may therefore also be true with respect to *S. murina*.

The egg index of *Osmia submicans* (0.71) also falls into the small category. This is an unexpected value since, for reasons suggested by Rozen (2003), there is a tendency for egg indices of cleptoparasitic bees to be substantially lower than those of their hosts (see ibid.: table 1). However, in this case, the close agreement in index values shared by *Stelis murina* and *S. elongativentris* suggests that the explanation might rest eventually on understanding why *O. submicans* has such small eggs.

DESCRIPTION OF MATURE OOCYTE

Mature oocytes (figs. 3, 5, 6) of *Stelis murina* were easily removed from the follicular tissue to reveal their shape, size, and translucent whitish color. Gently curved in lateral view (fig. 3), their front end was broadly rounded and in several cases somewhat bulbous, and their posterior end was more narrowly rounded. Their average length was 1.99 mm (N = 6), and their maximum diameter was 0.77 mm (N = 5). They appeared short (fig. 3) for their width compared with the eggs/mature oocytes of many other megachilids, e.g., *Osmia submicans* (fig. 4) and *Megachile nigripes* (Spinola) (Rozen and Kamel, 2007: figs. 11, 13). The chorion was



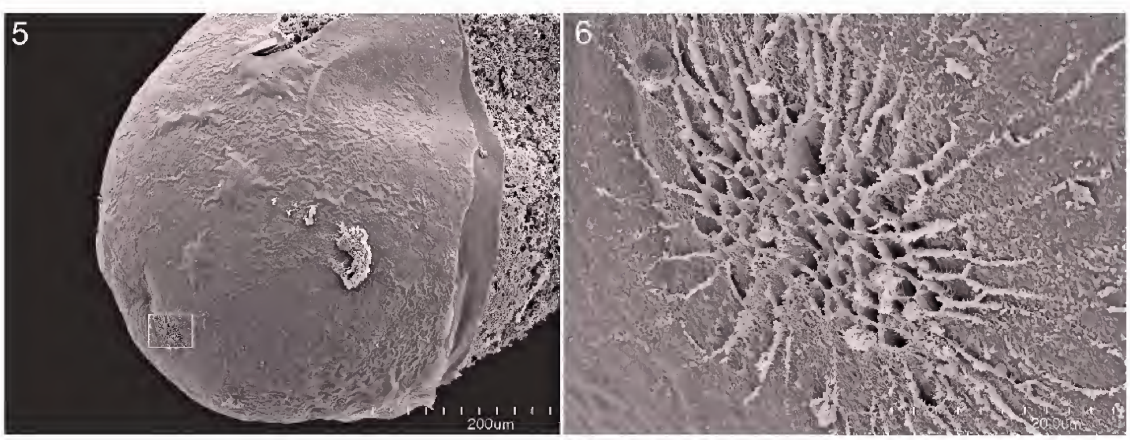
Figs. 3, 4. Mature oocytes of *Stelis murina* (**3**) and of its host, *Osmia submicans* (**4**), diagrammed from macrophotographs to the same scale (scale line = 1.0 mm), demonstrating similarity in volume and slight differences in shape; anterior ends to left.

shiny and seemingly smooth under stereoscopic examination.

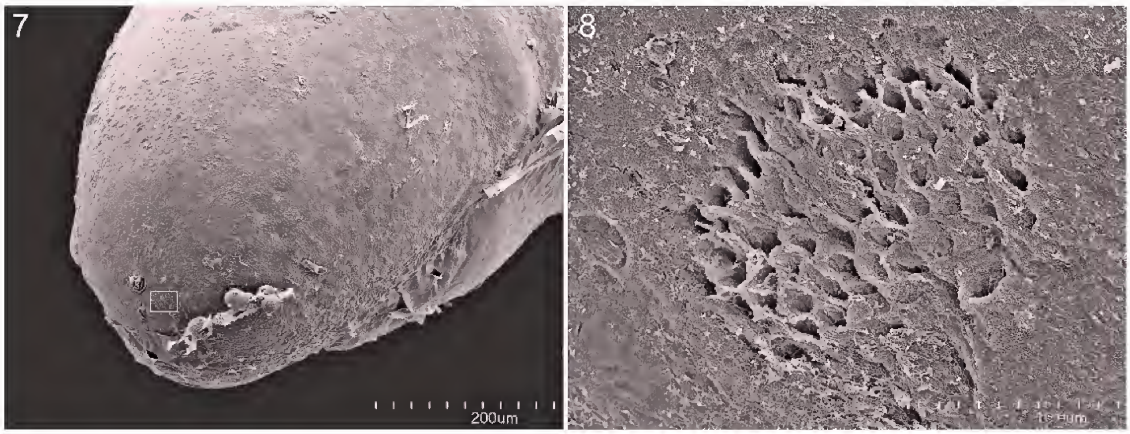
The mature oocytes of *O. submicans* (fig. 4) were similar to those of *S. murina* in that they were whitish and possessed a smooth, somewhat shiny chorion under stereoscopic examination. Their average length of 2.13 mm (N = 4) was somewhat greater than the 1.99 mm of *S. murina*, and the average maximum diameter of the mature oocyte of *O. submicans* was 0.67 mm, N = 4) compared to 0.77 mm, the average for *S. murina*. These are subtle differences, but suggest that the egg of the cleptoparasite is slightly more robust but shorter than that of the host, whereas the egg of the host is thinner but somewhat elongate. Their shapes differ in that the mature oocytes of *O. submicans* have anterior and posterior ends equally rounded (fig. 4) and the widest part of the oocyte is at, or posterior to, midlength, whereas the mature oocyte of *S. murina* possesses a rounded anterior end (fig. 3), which may even be bulbous in some cases, and their posterior part tapers before terminating in a narrowly round posterior end (fig. 3). The maximum diameter of the oocyte of *S. murina* is anterior to midbody and in some cases immediately behind the anterior end. The differences in shape of the eggs of host and cleptoparasite may be the best way of distinguishing them.

Although there are some differences in the dimensions of the mature oocytes of the host and cleptoparasite, we think that their volumes are probably nearly identical (compare figs. 3 and 4). The shortness of the oocyte of *Stelis murina* is balanced by its larger diameter. The difference in the egg indices of the two species is probably an artifact when assuming the linear dimensions of part of an organism (in this case egg length) is a true measure of its volume.

Under SEM examination three mature oocytes of *Stelis murina* revealed that most of the chorion was featureless except at the anterior pole where the micropyle consists of a faintly raised, small cluster of pores with elevated edges from which radiated thin elevated ridges in a reticulated pattern (figs. 5,



Figs. 5, 6. SEM micrographic of mature oocyte of *Stelis murina*. **5.** Anterior end, rectangle identifying position of micropyle. **6.** Close-up of micropyle identified by rectangle in fig. 5.



Figs. 7, 8. SEM micrographs of egg of *Osmia submicans*. **7.** Anterior end, rectangle identifying positions of micropyle. **8.** Close-up of micropyle identified by rectangle in fig. 7.

6). A single egg of *Osmia submicans* when examined with an SEM showed similar features except it lacked the pattern of elevated ridges radiating from the pores (figs. 7, 8).

The mature oocytes/eggs of almost all Megachilidae studied with an SEM to date have a smooth chorion with a micropyle consisting of a small cluster of pores at the anterior pole. Genera represented include: *Osmia* (present study), *Stelis* (Rozen, 2003; present study), *Coelioxys* (Rozen, 2003; Rozen and Kamel, 2007), *Megachile* (Rozen and Kamel, 2007), and *Radoszkowskiana* (Rozen and Kamel, 2007). An obvious exception is the egg of *Dioxys cincta* (Jurine) with its thick, nodular dorsal chorion contrasting with the smooth, fragile ventral chorion (Rozen and Özbek, 2003, 2005) (but not that of *D. pacifica* Cockerell [Rozen and Özbek, 2003]).

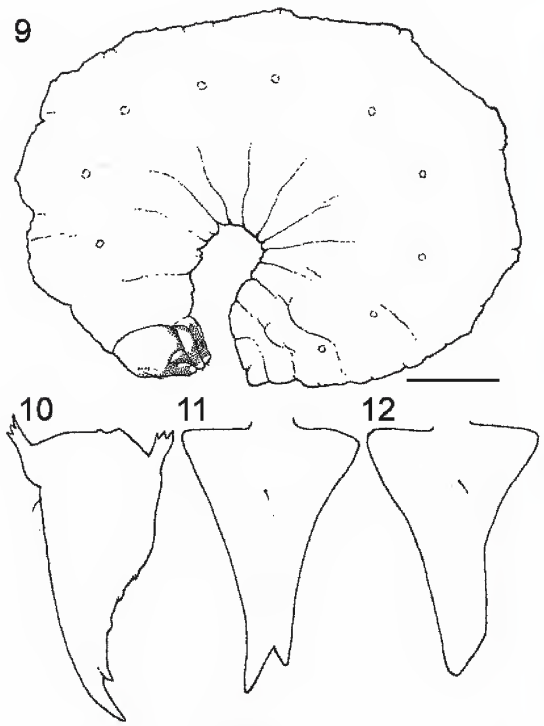
The mature oocyte of *Stelis murina* has no features that can be interpreted as cleptoparasitic adaptations such as chorionic modifications to resemble, or being inserted into, the brood-chamber wall, as found in the Nomadinae and some other cleptoparasitic Apidae (Rozen, 2003; Rozen and Özbek, 2003).

DESCRIPTION OF POSTDEFECATING LARVA OF *STELIS MURINA*

Figures 9–23

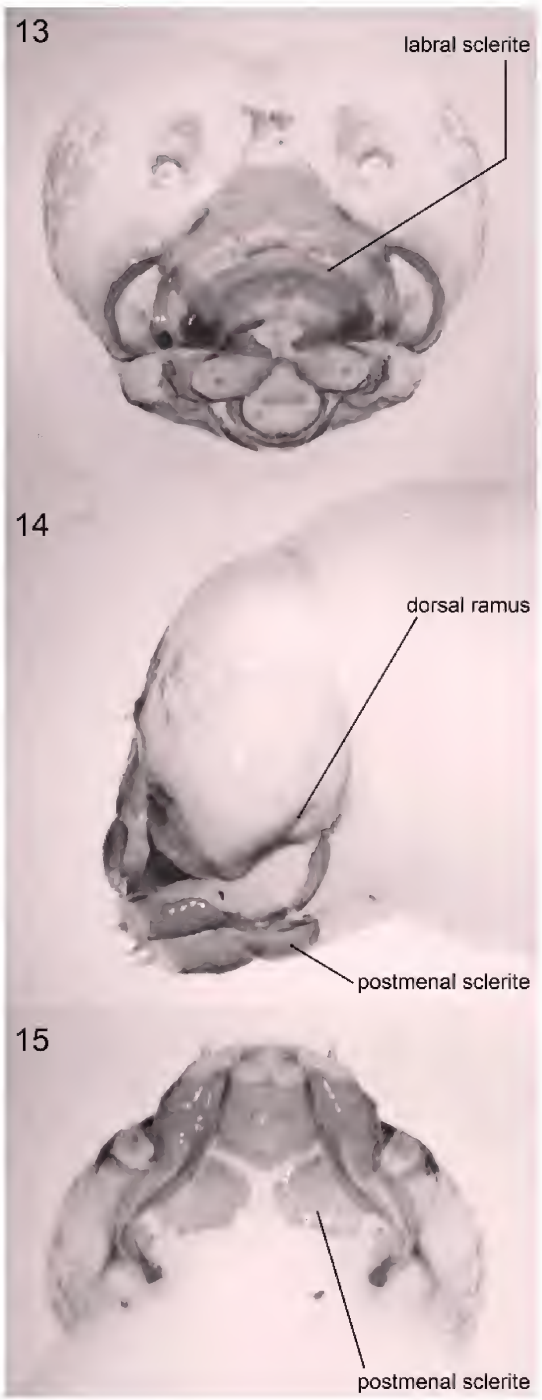
We compared the postdefecating larva of *Stelis murina* with larval specimens of *S. elongativentris*, *S. lateralis*, and the unidentified Parker, AZ, material. We also reviewed the published descriptions of the following: *Stelis chlorocyanea* (Rust and Thorp, 1973), *S. elongativentris* (Rozen, 1987), *S. lateralis* (Michener 1953, 1955; Rozen, 1987), *S. minuta* (Enslin, 1925), *S. nasuta* (Maneval, 1937), and *S. ornatula* (Micheli, 1935).

Diagnosis: Mature larvae of all known *Stelis* are typical of those of other megachilids in body shape and in possessing conspicuous body setae. There are, however, several distinguishing features. The one most visible is the extensive head pigmentation (especially on the mandibles, internal head ridges, and maxillary sclerites), which is perhaps best developed in *S. murina* (figs. 13–15). Unfortunately this coloring is somewhat fugitive on specimens after they are cleared, and the degree of pigmentation seems to vary from one species to the next, although it is more extensive than that found in other megachilids, including *Hoplostelis* (Rozen, 1966). Another feature is the lateral sclerotization of the postmentum (figs. 14, 15), a unique feature in mature bee larvae, although it is easily overlooked in some species because of reduction of pigmentation (e.g., *S. elongativentris*). Most species have mandibles that gradually taper from base either to a narrowly bidentate apex when view in outer or inner profile (*S. elongativentris*, Rozen, 1987: fig. 11; *S. ornatula*, Micheli, 1935: fig. 7; *S. murina*, figs. 11, 12) or to a simple pointed apex (*S. chlorocyanea*, Rust and Thorp, 1973: fig. 21, *S. lateralis* Michener, 1953: figs. 115, 116).

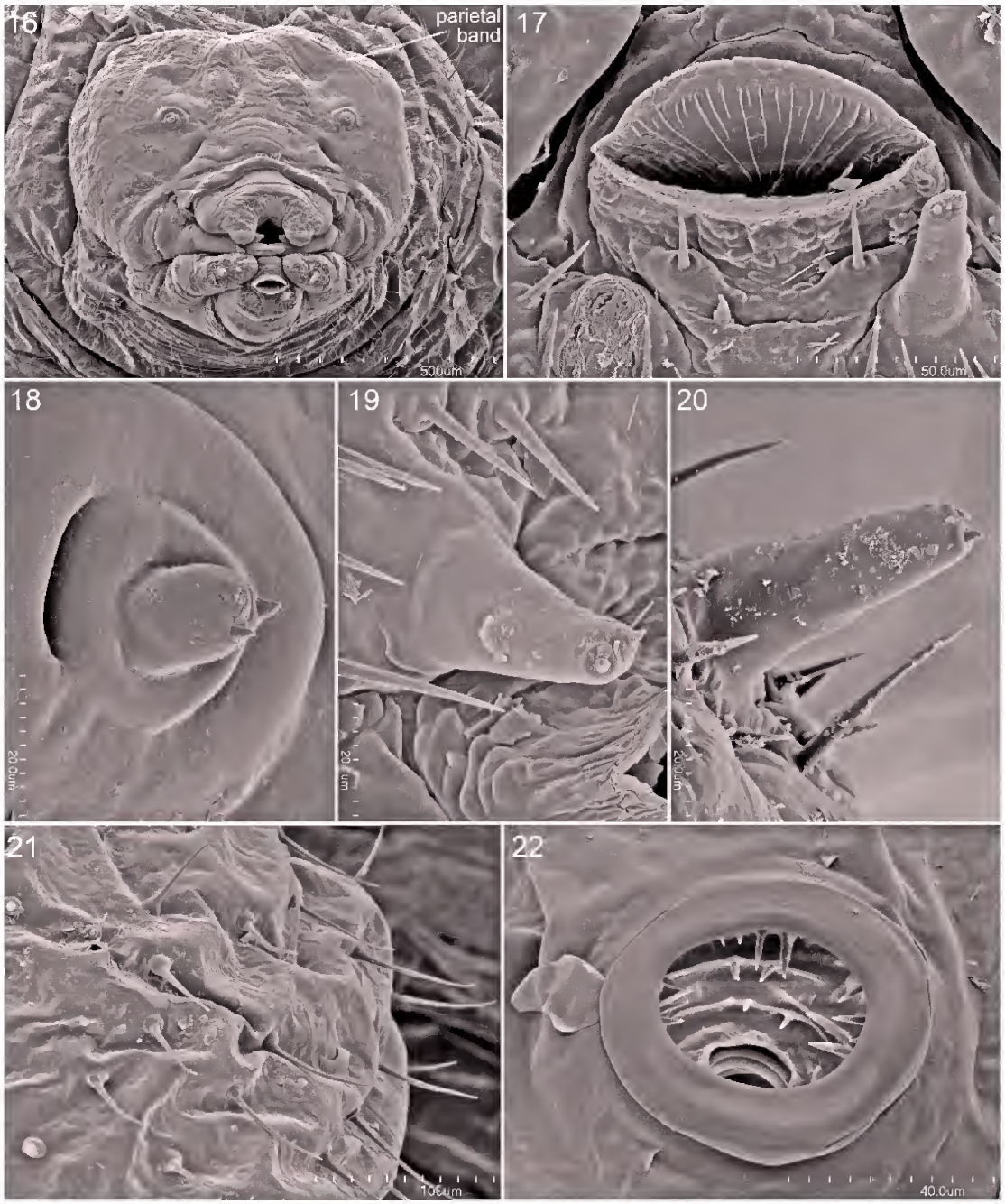


Figs. 9–12. Diagrams of mature larva of *Stelis murina*. **9.** Entire larva with setae omitted, lateral view; scale line = 1.0 mm. **10, 11.** Right mandible showing little wear, dorsal view and outer view (latter view with apex in maximum profile), respectively. **12.** Right mandible of another larva showing excessive wear, so that dorsal tooth completely absent and lower tooth greatly rounded, outer view. All mandibles to same scale. Scale line = 1.0 mm refers to fig. 9.

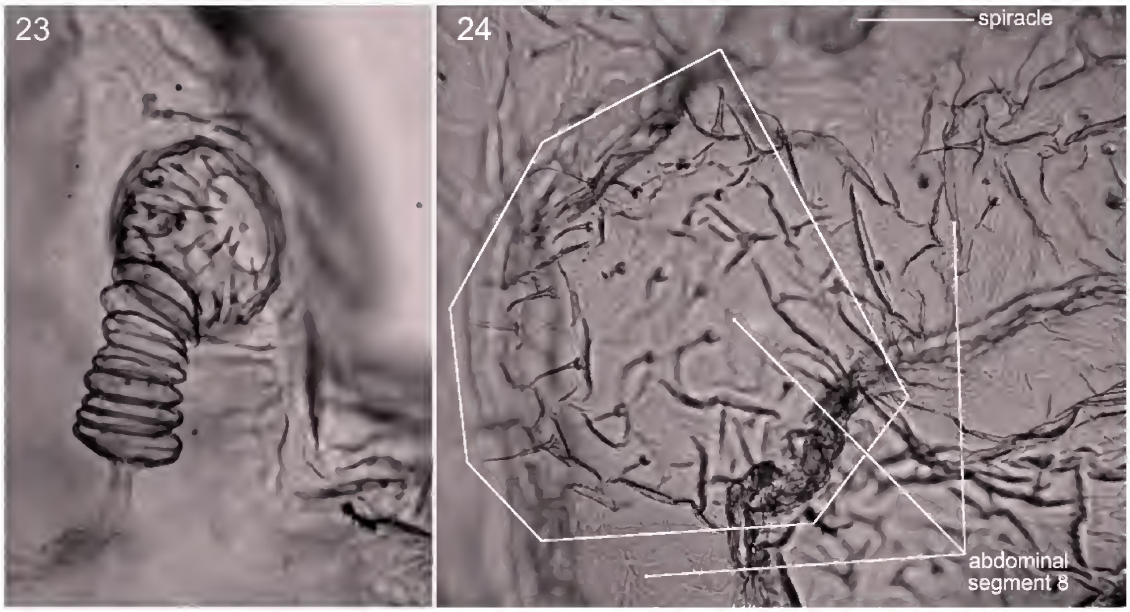
Bidentate mandibles always have the lower tooth larger whereas the smaller upper tooth varies in size and is usually subapical. Although the unidentified Parker, AZ, specimens also seem to have tapering mandibles, the upper tooth seems to be only slightly smaller than the lower one and is apical in position rather than subapical. The situation for *S. nasuta* (Maneval, 1937: figs 47, 48) is indeterminate, which is unfortunate because the larva is questionably hospicidal. A possible problem in using mandibular characters seems to be apical abrasion as exhibited at least in some *S. murina* (compare fig. 11 with fig. 12). The mature larva of *S. murina* is more pilose, with the pleural area of abdominal segment 8 bearing approximately 25 setae, than that of *S. elongativentris*, with fewer than 10 setae, but we lack comparable figures for other species.



Figs. 13–15. Macrophotographs of head of *Stelis murina*, showing pattern and configuration of pigmentation, frontal (**13**), lateral (**14**), and ventral (**15**) views.



Figs. 16–22. SEM micrographs of postdefecating larva of *Stelis murina*. **16.** Head, frontal view. **17.** Salivary lips (with right labial palpus broken), showing internal diverging ridges on lower surface of dorsal lip, frontal view from below. **18.** Right antenna (with one of three sensilla broken), semilateral view. **19.** Right labial palpus, semilateral view, at same magnification as fig. 18 to show that palpus is about twice as long as antennal papilla. **20.** Maxillary palpus, lateral view. **21.** Close-up of body setae on pleural swelling of abdominal segment 8, showing swollen setal bases and long, tapering shafts. **22.** Spiracle, showing narrow peritreme and concentrically directed atrial spines.



Figs. 23, 24. Macrophotographs of cleared specimen of *Stelis murina*. **23**. Spiracle, seen from inside body, showing spines on atrial wall and subparallel-sided subatrium. **24.** Pleural swelling of abdominal segment 8 (identified by polygon), showing abundant setae and position of spiracle.

DESCRIPTION: **Head** (figs. 13–19): Setae moderately long, tapering to fine points; those of parietals scattered, erect, with small alveoli; those of maxillary and labial apices straight, forward projecting and those of labral apex decumbent, downward directed. Following areas (figs. 13–15) tending to be heavily pigmented (compared to most bee larvae), with darker areas being very dark brown to nearly black (pigment fading with extensive boiling in aqueous solution of sodium hydroxide): internal head ridges (especially pleurostomal, hypostomal, and lateral parts of epistomal ridges), clypeus, area immediately above each antenna and smaller spots next to midline at same level, labrum, mandible, cardo, stipes, premental sclerite, large sclerotized area of each side of postmentum (figs. 14, 15); parietals with pigmentation pattern (figs. 13, 14) presumably reflecting internal scarring associated with muscle attachment (see Remarks). Integumental spiculation absent except for fine spicules on hypopharyngeal lobes and maxillary apices.

Parietals somewhat enlarged so that maximum lateral diameter of head capsule to maximum lateral diameter of foramen is 13:9; inner surface of integument of parietals on cleared head capsule scarred (see following section); area immediately above hypostomal ridge and just behind posterior mandibular articulation not produced as downward-directed tubercle, as present in many *Coelioxys* (Rozen and Kamel, 2007: fig. 47). Hypostomal ridge with dorsal ramus (fig. 14) that ends posteriorly partway to postoccipital ridge; anterior tentorial pit somewhat closer to basal ring of antenna than to anterior mandibular articulation in anterior view; epistomal ridge absent mesad of anterior tentorial pits; longitudinal thickening of head capsule (coronal ridge) present partway to level of antennae. Parietal bands almost completely obscured by integumental scarring when viewed with stereomicroscope but evident under SEM examination (fig. 16). Diameter of basal ring[4] of antenna small, about same as distance from outer edge of ring to center of anterior tentorial pit; antennal papilla (fig. 18) small,

[4] Because of the head-capsule pigmentation of this species, one can see that the basal ring of the antenna is actually the thickened, elevated edge of the parietal that encircles the presumably membranous antennal socket, from which the sclerotized antennal papilla arises. This feature is also present in *Stelis chlorocyanea* (Rust and Thorp, 1973: figs. 23, 25).

apically narrowly rounded, about equal in length to basal diameter, bearing three, tightly grouped sensilla. Apical margin of clypeus evenly curved, so that at midpoint its margin below level of anterior tentorial pits as seen in frontal view (fig. 16). Labral sclerite pigmented, transverse (fig. 13) with pigmentation extending into apical sensilla-bearing area; labrum apically membranous, unpigmented, without darkly pigmented median spot extending to apical labral margin as in *Coelioxys* (Rozen and Kamel: 2007: figs. 44, 45); apical labral margin broadly (fig. 13) to deeply (fig. 16) concave (variation suggesting that feature sensitive to preservation), with lateral apical angles rounded, pronounced; erect paired labral tubercles absent.

Mandible (figs. 10–12) elongate, apically attenuate, curved, slender, bidentate with ventral tooth fanglike when not abraded, much longer than dorsal tooth although dorsal tooth perhaps more prominent than that of *Stelis elongativentris* (Rozen, 1987: fig. 11; see Remarks, below); inner surface without projecting cusp as seen in dorsal or ventral views but faintly swollen, with coarsely irregular surface; outer surface with single seta not borne on tubercle; in outer view, mandible tapering from base to apex of lower tooth, suggesting that mandible could easily penetrate integument of another larva (but degree of tapering not as pronounced as that of *S. elongativentris* in outer view [ibid.: fig. 11]). Cardo and stipes well developed, very darkly pigmented; articulating arms of stipes broad, pigmented, extending just below hypopharyngeal lobe toward premental sclerite on each side; maxillary palpus (fig. 20) slender, elongate, more than two times longer than basal diameter, much longer than antennal papilla (fig. 18). Apex of labium rather slender, with pronounced dorsally projecting, median swelling above salivary opening; labium clearly divided into prementum and postmentum; premental sclerite elongate, darkly pigmented; postmentum with pair of large, darkly pigmented sclerites (see Remarks, below); labial palpi (fig. 19) subequal in length to maxillary palpi. Salivary lips projecting, broadly transverse, width about equal to distance between bases of labial palpi; inner surface of dorsal lip (visible only after specimen subjected to critical-point drying) with numerous subparallel, raised ridges diverging outward (fig. 17). Hypopharynx consisting of pair of well-separated, spiculate lateral lobes.

Body (figs. 9, 21–24): Body setae abundant, moderately short, and under high magnification (fig. 21) each with more or less swollen base that tapers immediately to long shaft that gradually, evenly tapers to fine apex; pleural area of abdominal segment 8 (figs. 21, 24) with approximately 25 setae;[5] integument without spicules. Body form robust with abdominal segments 4–7 larger than other segments; intersegmental lines weakly incised (due in part to confinement in cocoon); intrasegmental lines of most segments evident but faint on cleared specimen and not visible on uncleared specimens taken from cocoon (see fig. 9); paired body tubercles absent; intersegmental, middorsal body tubercles more or less (as in fig. 9) evident depending on preservation; pleural swellings weakly evident toward rear of body; abdominal segment 10 very short in lateral view, attached to approximate middle of segment 9 which is also short; anus transverse, projecting, positioned toward top of segment 10. Spiracles (figs. 21, 22) well sclerotized, faintly pigmented, subequal in size; somewhat shallow, globular atrium projecting beyond body wall, with distinct rim (fig. 21); peritreme moderately narrow, so that atrial opening about twice as wide as peritreme width; atrial inner surface with spines as long as width of peritreme, arranged in more or less concentric rows; these spines direct inward at right angles to atrial wall; primary tracheal opening with collar; subatrium moderately short, with perhaps 7–12 chambers (numbers varying from spiracle to spiracle on same individual); externally subatrial chambers of approximately uniform diameter from outer- to innermost chamber (fig. 23) (i.e., sequence of chambers not tapering from outer- to innermost). Male of cleared specimen with median, transverse integumental scar close to posterior margin; female sex characters unknown.

[5] The approximate number of setae on the pleural swelling of abdominal segment 8 seems to be a good index of the abundance of body pilosity among megachilid larvae, in part because that swelling is generally well defined even on larvae constrained by tight-fitting cocoon walls.

MATERIAL STUDIED: All from Egypt and all postdefecating larvae, recovered from their cocoons: 1 larva: Ismailia: Suez Canal University, IX-17-2006 J.G. Rozen, S.M. Kamel); 1 larva: same except IX-19-2006, from nest of *Osmia submicans*; 2 larvae: same as previous except IX-21-2006 (J.G. Rozen, S.M. Kamel, M. Shebl); 2 larvae: same as previous except (IX-20-2006); 1 larva: Ismailia Experiment Station, V-6-2007 (J.G. Rozen, S.M. Kamel).

REMARKS: Some of the larvae of *Stelis murina* showed signs of mandibular wear, so that the lower, longer apical tooth was considerably reduced almost to the point of being no longer than dorsal tooth and on one specimen the mandible was so badly worn that it appeared to end as single apical tooth (fig. 12). The cause of wear is difficult to explain since host cells are not lined with soil or other highly abrasive materials. However, Rozen and Kamel (2009) noted changes in mandibular shape in *Sapyga luteomaculata* when comparing early and late stage last (fourth) instars that suggested similar (but less extensive) mandibular wear.

The large sclerotized (and pigmented) paired postmental sclerites are remarkable features not found in any other bee genus to date. They were originally discovered by Rust and Thorp (1973: table 2) on *Stelis chlorocyanea*, but other features, such as their shape, were not described. In the case of *S. murina*, each sclerite is large and very darkly pigmented. They approach one another along the labium's midline but do not join. However, each is completely fused laterally with the maxillary stipes, so that, as the stipes extends forward through the straightening of the cardo-stipes axes, the postmentum also thrusts forward. Whether this is the adaptive function of the postmental sclerotization is unknown since the armor cladding of the postmental area might also be explained as defensive against the attack of other larvae.

We have reexamined the postmentum of a postdefecating specimen of *Stelis elongativentris* studied by Rozen (1987). Head pigmentation of that species is far less than on *S. murina*, and as noted by him it is faintly sclerotized and pigmented. However, examination of a completely colorless specimen of *S. lateralis* studied by Michener (1953) gave no hint of postmental sclerotization, although it had been cleared, perhaps resulting in lost pigmentation. On the other hand the three specimens of the unidentified Parker, AZ, material showed a large, faintly tinted, reflective postmental sclerite fused to the stipes on each side of the head.

HOSPICIDAL ADAPTATIONS OF MATURE LARVA: We think that the following anatomical features of *Stelis murina* (as well as of other *Stelis* species) are modifications that enable the larva to assault and kill the host larva and larvae of competing cleptoparasitic individuals. The tapering mandibles are the main weapons with their elongate, fanglike ventral tooth while the smaller dorsal tooth is either positioned subapically or (in some other species) entirely absent.

The enlarged, somewhat globose parietals with integumental scarring are associated with the strong mandibular musculature. Enlargement of the parietals allows more area for the origin of mandibular musculature. The scarring was noted by Rozen (1987) for *Stelis lateralis* and *S. elongativentris*. For want of a better term, we use the term "scarring" to denote the peculiar uneven appearance of the integument of the parietals, which is evident in *S. murina* because of the accompanying pigmentation (figs. 13, 14). It may possibly represent a latticework-like internal thickening of the integument where individual muscles attach. The SEM micrograph of the parietal does not show any external evidence of the thickening (fig. 16). This latticework possibly strengthens the entire parietal and thus may function to provide a firm base for the contraction of the mandibular muscles, which would enable the mandibles to close forcefully to destroy the opponent. Whether the sclerotization of the postmentum can be considered an adaptation associated with hospicidal behavior is uncertain, as indicated above.

It is instructive to compare these features with those of the cleptoparasitic *Hoplostelis bilineolata* (Rozen, 1966), whose larva does not play a role in disposing of the host egg or larva (Bennett, 1966). In *H. bilineolata*, the mandibles bear a scoop-shaped apical concavity and are not modified by tapering apically and not fanglike in shape (figs. 6–8); the head, with a maximum lateral diameter of head capsule to

maximum lateral diameter of foramen ratio of 7.5:7.0 is not enlarged; the integument of the parietals is normally smooth; and there is no postmental sclerotization.

Unanswered questions include the extent to which the features of *Stelis* identified to be hospicidal appear in earlier instars and, if they do, are they found in all instars or just certain ones. It is hoped that future studies of *S. murina* or other exemplars of the genus will address this matter.

PRELIMINARY KEY TO MATURE LARVAE OF CLEPTOPARASITIC MEGACHILIDAE

We present here a key to the mature larvae of cleptoparasitic Megachilidae, thus providing an update to Rozen's (2001) key to the mature larvae of all available cleptoparasitic bees. Information for this key is derived not only from the current investigation and the 2001 study but also from recently published accounts of *Dioxys* (Rozen and Özbek, 2005) and *Radoszkowskiana* and *Coelioxys* (Rozen and Kamel, 2007, 2008). This key is, of course, provisional since it is based on only a few exemplar taxa whose mature larvae are available. Furthermore, it completely omits cleptoparasitic taxa, such as *Hoplitis* (*Bytinskia*), *Euaspis*, and many of the genera of the Dioxyini, whose larvae are unknown. Because degree of pigmentation is diagnostic in some cases, the key is primarily intended to distinguish uncleared, postdefecating larvae; pigmentation is most intense after defecation and clearing often reduces pigmentation.

As pointed out by Rozen (2001) mature cleptoparasitic megachilid larvae can be separated from those of cleptoparasites in other families by the following: integument of head and at least of anterior body segments (but usually on all segments) with elongate setae; labral sclerite present, strongly transverse, usually more or less pigmented; transverse salivary opening on projecting lips; abdomen often with midline intersegmental dorsal tubercles. Of these features, the body setae are the most reliable and most easily observed (but are characteristic only of last larval instars).

1. Apical margin of labrum with large, median dark area extending from labral sclerite to apical edge, contrasting with pale, unpigmented apical margin on each side (Rozen and Kamel, 2007: figs. 44, 45); conspicuous hypostomal tubercle projecting ventrally from vicinity of posterior mandibular articulation often but not invariably present (ibid.: fig. 47); distribution worldwide . . . . . *Coelioxys*

– Apical margin of labrum without dark median spot distinct from pale lateral apical margin; hypostomal tubercle absent (Rozen and Kamel, 2007: figs. 44, 45) 2

2. Antennal papilla longer and more robust than maxillary and labial palpi (except in *D. cincta*, whose antennal papilla is about equal in size to maxillary palpus) (Rozen, 2001: fig. 19); distribution Palearctic as far east as Central Asia, North Africa, and western North America (Michener, 2007) . . . *Dioxys*

– Antennal papilla shorter than either maxillary or labial palpi (Rozen and Kamel, 2007: fig. 47) 3

3. Mandibular apex in adoral view obliquely truncate, irregularly serrated (Rozen, 1966: fig. 7); mandible with pronounced apical concavity (ibid.: figs. 7, 8); internal head ridges normally pigmented; distribution Neotropical (Michener, 2007). . . *Hoplostelis*

– Mandibular apex in adoral view apically nonserrate, with ventral tooth sharply pointed, elongate and dorsal tooth smaller, subapical (fig. 10, 11; Rozen, 1987: figs. 10, 11) to absent (Michener, 1953: figs. 115, 116; Rust and Thorp: 1973: figs. 20–22) 4

4. Internal head ridges darkly pigmented, parietals with pigmented patches, and clypeus often pigmented (figs. 13–15); usually lateral postmental sclerites evident (fig. 15); parietal somewhat swollen, bearing scarring associated with muscle attachment; distribution worldwide except Australia and South America south of Colombia . . . . . *Stelis*

– Internal head ridges less darkly pigmented, and parietals and clypeus without pigmentation (Rozen and Kamel, 2007: fig. 43); postmental sclerotization absent; parietals not swollen nor scarred; distribution North Africa to Central Asia (Schwarz, 2001) . . . . . *Radoszkowskiana*

OVERVIEW OF THE KNOWN MODES OF CLEPTOPARASITISM IN MEGACHILIDAE

With cleptoparasitic bees, the term mode of cleptoparasitism refers to a number of phenomena associated with (1) the cleptoparasite

gaining entrance into the host cell, (2) the avoidance of detection of cleptoparasite egg by host female, and (3) the elimination of the host offspring and competing cleptoparasites. These phenomena are addressed by finding answers to the following questions. With respect to gaining entrance into the host cell, does the cleptoparasite do so while the cell is still open or after the host female has sealed the cell? Does the cleptoparasitic female remain in, near, or by the entrance of, the host nest and attack brood cells as they become available during the process of cell construction, foraging, and egg deposition, or does she travel from one nest to another in search of appropriate cells? With respect to eliminating the host immature, does the cleptoparasitic female do this, and if so does she use her mandibles or her sting (or metasomal apex)? If the cleptoparasite larva kills the host, at what stage(s) of the cleptoparasitic immature and at what stage(s) of the host's development? What anatomical modifications enable the cleptoparasite to do this? Or is the host offspring eliminated by being starved, i.e., out-competed by the developing cleptoparasite(s)? If the host cell is still open when attacked, how is the cleptoparasite egg hidden from the returning host female (assuming that a discovered parasite egg would be killed by the host female)? If the host cell is already closed when attacked, how does the parasite insert her egg into the cell? Does she remove the closure, insert her egg, and close it again, or does she make a small hole and insert her egg through the opening? Only if these questions are answered for a particular cleptoparasite we can then state that we understand its mode of parasitism. Among the total range of cleptoparasitic bees, all of these phenomena are known or are suspected.

However, among Megachilidae, we can summarize what is known about each of the following in addition to *Stelis* whose mode of cleptoparasitism (to the extent understood) is summarized above: *Coelioxys*, *Radoszkowskiana*, *Dioxys*, and *Hoplostelis*.

Coelioxys: Two modes of cleptoparasitism have been identified so far. The most common (Baker, 1971; Rozen and Kamel, 2007) involves the female *Coelioxys* entering the host cell while it is being provisioned, hiding her egg between the layers in the leaf-lined wall or in the provisions. The first two larval instars develop on the provisions, and the third instar with a nearly fully sclerotized, prognathous head and huge mandibles, kills the host larva. The last two instars have a more normal anatomy and feed in the provisions.

In the other mode, so far restricted only to the subgenus *Allocoelioxys* (Ferton, 1896; Rozen and Kamel, 2008), the female *Coelioxys* enters the host cell while still open but after the host egg has been deposited. She deposits her egg on top of the host egg presumably while the host is gathering closure material. The parasite embryo develops before that of the host, and its first instar, still surrounded by chorion, bites into the host egg with sharply curved mandibles and ingests its contents, thereby killing it. Subsequent parasite instars have the normal anatomy of a provisions-feeding bee larva.

Radoszkowskiana: The only species of this genus studied to date (Rozen and Kamel, 2008) has the same mode of parasitism as does the subgenus *Allocoelioxys* described above. This would seem to suggest that *Coelioxys* and *Radoszkowskiana* had a common cleptoparasitic ancestor, and that this mode is the primitive state.

Dioxys: This is another genus that seems to have at least two modes of cleptoparasitism. In the first to be investigated (Rozen and Favreau, 1967: fig. 4; Rozen, 1967), the cleptoparasitic egg of *D. pomonae* was inserted through the cell lining composed of masticated leaves into a closed cell containing a host egg. Though considerably smaller than the host egg, its egg index (Rozen and Özbek, 2004) placed it in the *small* category of Iwata and Sakagama (1966). The egg was an ordinary little white "sausage" with no distinctive chorionic ornamentation.

The second mode of cleptoparasitism was exhibited by *Dioxys cincta*, and was first detected when its mature oocyte was examined (Rozen and Özbek, 2003: figs. 1–6.). It was very small and categorized as dwarf. Its unusually thick and nodular dorsal chorion contrasted with the thin, smooth ventral chorion and suggested that the egg would eventually be found deposited limpetlike against the wall of a brood cell, as indeed

was the case several years later (Rozen and Özbek, 2005: figs. 1, 2). Thus, this species deposits its egg before cell closure, and its egg is afforded protection because of small size and exposed dorsal chorion textured like the brood chamber wall.

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